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## Mating Systems of Chaetodontid and Pomacanthid Fishes at St. Croix

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*With 3 figures*

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### Abstract

Reproductive behavior and mating systems of two Caribbean chaetodontids, *Chaetodon aculeatus* and *C. capistratus*, and one pomacanthid, *Holacanthus tricolor*, were investigated at St. Croix. Sexual dimorphism in size, the abundance and distribution of fishes and their prey, and foraging and grouping patterns were examined. Differences in mating systems between species are related to differences in resource abundance and distribution, foraging patterns, and type of sex determination.

*Chaetodon aculeatus* foraged solitarily during the day and mated a nearby individual at dusk. Pair formation occurred several evenings without spawning. *C. capistratus* was monogamous, and pairs foraged together in a home range during the day. Each pair spawned only once per evening, and it appeared that reproduction occurred at the same site each evening. *Holacanthus tricolor* foraged solitarily during the day on male territories. *H. tricolor* was a polygynist, and a dominant male spawned with up to three females, but females spawned only once per night.

### Introduction

Unlike other vertebrates which are generally gonochoristic (having separate sexes), teleost fishes exhibit a complete range of hermaphroditic characteristics (protandry, protogyny, and synchronous hermaphroditism). For coral reef fishes hermaphroditism appears to be a common sexual mode (ATZ 1964; REINBOTH 1974; SMITH 1967, 1975).

While reproductive behavior and mating systems of coral reef fishes, in particular, are poorly known, families on which data exist (Labridae: ROBERTSON 1972; WARNER et al. 1975; ROBERTSON and HOFFMAN 1977; ROSS 1981;

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Pomacentridae: MOYER and BELL 1976; ROSS 1978; Serranidae: SHAPIRO 1979; 1981; Scaridae: CHOAT and ROBERTSON 1975; WARNER and DOWNS 1977) reveal variable patterns of sequential hermaphroditism.

Although chaetodontids and pomacanthids were once classified in the same family, they are not so close phylogenetically (FREIHOFER 1963; BURGESS 1974). They are reproductively similar in that they spawn planktonic eggs up, away from the reef, at dusk. Because of their ecological similarities as well as their potential differences in reproduction (monogamy versus polygyny), we compared the reproductive behavior and mating systems of two Caribbean chaetodontids (*Chaetodon aculeatus* and *C. capistratus*) and three pomacanthids (particularly *Holacanthus tricolor*, and incidentally *Pomacanthus arcuatus* and *P. paru*) at St. Croix, US Virgin Islands.

#### A. Pomacanthidae (Angelfishes)

Pomacanthid fishes generally occur as solitary individuals or in pairs, and exhibit three basic foraging patterns. Large species such as those of *Holacanthus* and *Pomacanthus* are benthic carnivores that feed primarily on sponges, but sometimes take ascidians, fish eggs, gorgonians and zooantharians (RANDALL and HARTMAN 1968; HOBSON 1974; pers. obs.). Smaller species, particularly of *Centropyge*, are herbivores (HIATT and STRASBURG 1960; HOBSON 1974; RANDALL 1967). The third foraging pattern is displayed by *Genicanthus* species which are planktivores that take pelagic ascidians in mid-water, supplemented by some benthic invertebrates (SHEN and LIU 1976; ALLEN 1980). Since food resource distribution is probably a critical parameter influencing mating systems (VERNER and WILLSON 1966; ROBERTSON and HOFFMAN 1977; WARNER and HOFFMAN 1980), and our current knowledge of pomacanthid reproduction is based on the herbivorous and planktivorous genera, it is not clear whether the larger benthic feeding genera should exhibit similar mating systems or not.

Pomacanthid spawning behavior is known from field observations of *Centropyge* species in Hawaii (LOBEL 1978) and Japan (MOYER and NAKAZANO 1978) and from aquaria observations of *Genicanthus* species in Taiwan (SHEN and LIU 1976) and Japan (SUZUKI et al. 1979). These studies indicated that species of *Centropyge* and *Genicanthus* spawn planktonic eggs at sunset and exhibit harem polygyny as well as protogynous hermaphroditism. The largest individual of a group is a single male, and is dominant over the females (LOBEL 1978; MOYER and NAKAZANO 1978). Adults remain at a particular site for life where they breed and feed. Upon death or removal of the male, the largest female changes sex to take his place (MOYER and NAKAZANO 1978). There is no published information on reproductive behavior or mating systems of the remaining five pomacanthid genera (*Apolemichtys*, *Chaetodontoplus*, *Holacanthus*, *Pomacanthus* and *Pygoplites*).

#### B. Chaetodontidae (Butterflyfishes)

Most chaetodontids are diurnal carnivores that exhibit three main foraging patterns: corallivores, benthic omnivores, and planktivores. Many *Chae-*

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*todon* species are corallivores (REESE 1977; NEUDECKER 1977; BIRKELAND and NEUDECKER 1981) and have been further classified as grazers, browsers and corallum feeders (NEUDECKER 1979). Remaining *Chaetodon* species are omnivores that prey on corals, crustaceans, fish eggs, gorgonians, polychaetes and zooanthids (HIATT and STRASBURG 1960; HOBSON 1974). Dietary generalization has been compared to prey abundance for two such species in the Caribbean (BIRKELAND and NEUDECKER 1981). Finally, the genera *Hemitaenrichthys* and *Heniochus* feed on plankton in midwater (HOBSON 1974; ALLEN 1980: 327). Many adult chaetodontids appear to remain in one home range for life (REESE 1973; NEUDECKER, pers. obs.) where they feed on benthic prey. Consequently, mates, food, and shelter are all potentially defensible.

Reproductive behavior of chaetodontids is known only from ancillary observations of three species in Hawaii (LOBEL 1978) and from aquarium observations in Japan (SUZUKI et al. 1980). However, considerable work has been done on chaetodontid social behavior (REESE 1973, 1975, 1977; EHRLICH et al. 1977), and foraging patterns (HIATT and STRASBURG 1960; HOBSON 1975; NEUDECKER 1977, 1979; BIRKELAND and NEUDECKER 1981). Together, those reports suggest that several species of butterflyfishes are monogamous gonochores and may therefore be an exception to the pattern of coral reef fish hermaphroditism.

## Methods

### A. Data Sources

Five sources of data are the basis for our analyses: 1) Observations during National Undersea Laboratory System (NULS) Saturation Mission 78-1 in May and June 1978 during 13 scuba excursions (38 h by NEUDECKER) from underwater habitat Hydrolab at St. Croix; 2) Most observations reported herein were made during NULS Mission 80-1 (February–March 1980) in 13 scuba excursions (70 h for two aquanauts); 3) 40 h of observations were made on Buck Island Channel Patch Reefs after Mission 80-1 at St. Croix; 4) Data on sexual dimorphism of chaetodontid and pomacanthid fishes were taken from specimens collected on site and 5) from museum specimens.

### B. Study Site Descriptions

#### 1. Salt River Canyon

The Hydrolab is located on a sand bottom in Salt River Canyon in 15.5 m of water, about 30 m north of the barrier reef fronting Salt River Estuary and about 5 m west of the eastern slope (Fig. 1). Observations in Salt River Canyon were made at four 100 m transect lines established in 1978 along the 15 and 30 m isobaths on the east slope and west wall, by BIRKELAND and NEUDECKER (1981). Spawning observations were made at a submarine buttress in 18 m of water on the east slope.

The west wall of the canyon is steep to vertical in many places, and has overhangs, caves, and crevasses. Scleractinian corals are more prevalent on the west wall at both 15 and 30 m than on the east slope at either depth (BIRKELAND and NEUDECKER 1981). Most coral species are more abundant at 15 m at both locations, except *Agaricia* which is more prevalent at 30 m (BIRKELAND and NEUDECKER 1981). Consequently, west wall sites had a greater abundance and diversity of resources used by the fishes we studied.

The eastern slope is characterized by a gentle slope of 15–20° and has more unconsolidated sediments. Rounded coral cobbles blanketed by a layer of carbonate sand are

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the substratum and form sediment trails running down to the canyon floor. Gorgonaceans are more common on the eastern slope at both depths and corals are less abundant than on the west wall. Most spawning observations were made at a buttress in 18 m of water on the east slope.

## 2. Patch Reefs

The three Buck Island Channel patch reefs are located between St. Croix and Buck Island. These reefs are about 2 km north of Coakley Bay and about 700 m west of Buck Island (Fig. 1). The reefs are between 7 and 11 m deep and are covered predominantly by *Acropora cervicornis* coral and *Pseudoplexaura gorgonida*. The reefs range in size from 100 to 200 m<sup>2</sup> and are bordered by sand.

## C. Observations Techniques

### 1. Abundance and Distribution of Fish and Prey

Abundance of chaetodontid and pomacanthid fishes was measured by several censuses along the four transect lines. All fishes seen within 1 m to either side and within 2 m above

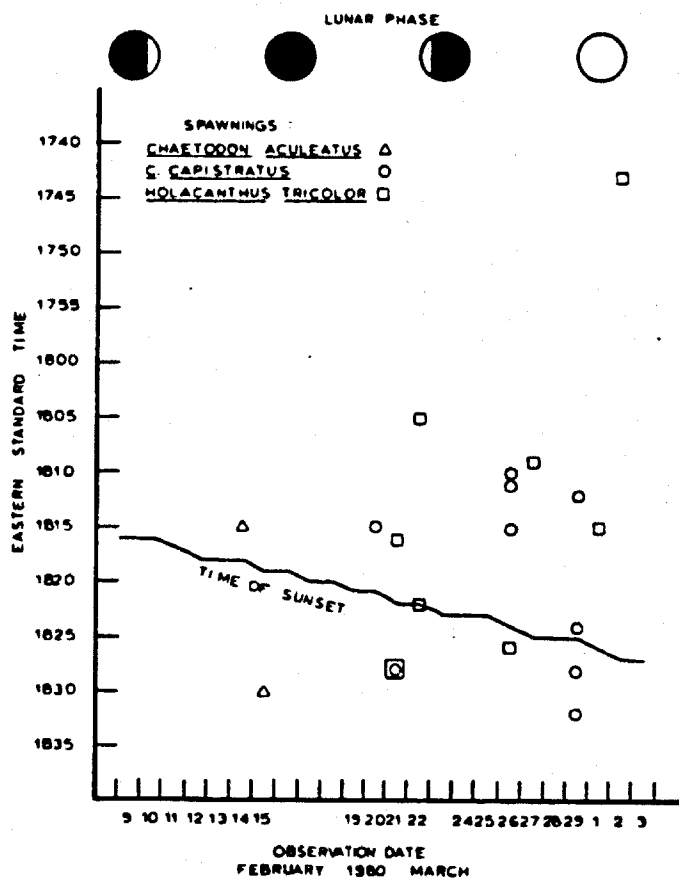


Fig. 1: Map of St. Croix, U.S.V.I., showing Salt River Canyon and the Buck Island Patch Reefs

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the transects were counted for a sample area of 200 m<sup>2</sup> or 400 m<sup>2</sup>. Relative abundance of prey species along the transects was measured in terms of surface area available to the fish by BIRKELAND and NEUDECKER (1981).

### 2. Grouping and Use Patterns

Observations of grouping patterns were noted by classifying the social status of each individual followed for 5 min during an investigation of their foraging patterns (BIRKELAND and NEUDECKER 1981, NEUDECKER data) and from individuals counted in the censuses. A species was determined territorial or home-ranging by its use patterns and species interactions. Home range sizes were also estimated from the foraging observations of *Chaetodon capistratus* (N = 85) and *C. aculeatus* (N = 67). We have less information on the territory sizes of *Holacanthus tricolor* but know that a harem remained at a specific site for at least two years, and harems were stable for the duration of our 1980 observations.

### 3. Size Dimorphism

We collected 28 specimens at Salt River Canyon in 1978 (*Chaetodon aculeatus*, N = 12; *C. capistratus*, N = 11; *Holacanthus tricolor*, N = 6). For an analysis of size (SL = standard length) dimorphism ( $\bar{X}$  SL ♂ /  $\bar{X}$  SL ♀). Juveniles (sexually immature) were excluded from the analysis. We acquired additional data from specimens loaned by Dr. James BÖHLKE, Chairman and Curator of Ichthyology, Academy of Natural Sciences of Philadelphia and from David J. GORDON, of the Museum of the University of Miami Rosenstiel School of Marine and Atmospheric Sciences. Because samples were collected randomly without regard to pairs or harems, sex ratios are probably not indicative of those that prevail on the reef.

### 4. Reproductive Behavior

Observers were on site slightly more than 1 h before sunset so that the entire spawning event could be observed. Specific individuals and pairs were recognized by unique color or morphological variations and by their repeated presence at particular places. Observations were conducted from distances of less than 4 m and data were recorded on underwater slates. Observers were stealthy and attempted to hide themselves between topographical features of the reef or by lying still on the bottom. Thus we were either unseen by the spawners or our presence did not disrupt their normal reproductive behavior. During the 20 evenings of observations (abscissa, Fig. 1), underwater visibility was always greater than 10 m. When courtship began we recorded the time, location, and general behavioral sequences. Spawning events were also photographed with 35-mm and super-8 cameras. Reported times are Eastern Standard Time. Configurations of the moon and times of sunset for St. Croix were obtained from the 1980 American Ephemeris and Nautical Almanac (U.S. Government 1979).

## Results

### A. *Chaetodon capistratus*

#### 1. General Ecology

*Chaetodon capistratus* is abundant on reefs throughout the western Atlantic, and in Salt River Canyon exhibited a mean abundance of  $2.2 \pm 1.6$  individuals/200 m<sup>2</sup>, and accounted for 47 % of the fishes counted (Table 1). *C. capistratus* is a browser of anthozoans and prefers hexacorals, especially scleractinians, over octocorals and antipatharians (BIRKELAND and NEUDECKER 1981). This butterflyfish occurs mostly in pairs (Table 2) which forage and rest in specific home ranges.

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## 2. Size Dimorphism

Males of *C. capistratus* tend to be slightly larger than females (Table 3). *Chaetodon* species occur mostly as male-female pairs of individuals of approximately equal size (REESE 1975; pers. obs.). Because pairs appear to be permanent and remain in one area of the reef for life (REESE 1973, 1975), we suspect that individuals pair while small and grow at similar rates. Consequently, when fishes are collected indiscriminately, and not in pairs, some females are larger than males, resulting from different ages or growth rates between pairs. Growth rates and pair size may also be related to habitat, food abundance, and quality which is partly reflected by geographical variance in size dimorphism (Table 3).

Table 1: Abundance and distribution of chaetodontid and pomacanthid fishes and surface areas of major resource groups at Salt River Canyon in 1978. Fishes were quantified by counting all individuals within 1 m to either side of and within 2 m above 100 m transect lines. Data are presented as average percentage of total number of chaetodontids and pomacanthids at each transect. Resource distribution is reported as the percentage of surface area of resources counted and the numbers of colonies measured (after BIRKELAND and NEUDECKER 1981). SE = standard error

Fishes (% of total)	West Wall		East Slope	
	15 m	30 m	15 m	30 m
<b>Chaetodontidae</b>				
<i>Chaetodon aculeatus</i>	15	38	9	31
<i>C. capistratus</i>	67	28	63	31
<b>Pomacanthidae</b>				
<i>Molacanthus ciliaris</i>	2	0	0	0
<i>M. tricolor</i>	9	30	9	0
<i>Pomacanthus arcuatus</i>	7	6	19	38
$\bar{x} \pm SE$ Number of fishes	$7.9 \pm 1.5$	$5.9 \pm 0.8$	$3.8 \pm 0.4$	$3.3 \pm 1.1$
(N) transects	(7)	(8)	(9)	(14)
<b>Resources % (N)</b>				
Plexaurids	44 (22)	4 (4)	84 (75)	80 (75)
Scleractinians	20 (283)	33 (41)	13 (122)	>1 (16)
Sponges	1 (27)	5 (15)	>1 (7)	1 (12)
Antipatharians	29 (2)	55 (26)	0	15 (7)
% of Total	92	97	98	97

Table 2: Grouping patterns of chaetodontid and pomacanthid fishes in Salt River Canyon during the day. Groups are composed of three or more individuals

	Solitary (N)	Paired (N)	Grouped (N)
<b>Chaetodontidae</b>			
<i>Chaetodon aculeatus</i>	91 % (61)	8 % (6)	0
<i>C. capistratus</i>	15 % (13)	75 % (64)	10 % (8)
<b>Pomacanthidae</b>			
<i>Molacanthus ciliaris</i>	100 % (5)	0	0
<i>M. tricolor</i>	100 % (48)	0	0
<i>Pomacanthus arcuatus</i>	43 % (6)	57 % (8)	0
<i>P. paru</i>	0	100 % (4)	0

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**Table 3:** Size dimorphism of adult chaetodontid and pomacanthid fishes from the Caribbean. Since pairs or harems were seldom collected together, individuals were lumped by sex, and mean standard lengths (SL) were compared for local size dimorphism. Mean ( $\bar{X}$ ) size dimorphism ( $\bar{X}$  SL male/ $\bar{X}$  SL female) for each species was calculated as the average of local populations. Museum specimens and data are from (1) the Academy of Natural Sciences of Philadelphia, and (2) the University of Miami. SD = standard deviation

	Collection sites	Males $\bar{X} \pm SD$ (N) SL (mm)	Females $\bar{X} \pm SD$ (N) SL	Local size dimorphism	Species $\bar{X} \pm SD$ size dimorphism
<b>Chaetodontidae</b>					
<i>Chaetodon ocellatus</i>	Salt River Canyon	67 $\pm$ 2 (8)	64 $\pm$ 2 (4)	1.05	
	Bermuda, Grand Cayman, Jamaica <sup>1</sup>	73 $\pm$ 6 (3)	72 $\pm$ 9 (3)	1.01	1.07 $\pm$ 0.07
<i>C. capistratus</i>	Florida, Bahamas, Columbia <sup>2</sup>	57 $\pm$ 11 (6)	50 $\pm$ 4 (8)	1.14	
	Salt River Canyon	91 $\pm$ 6 (3)	86 $\pm$ 9 (4)	1.06	
	Santa Catalina, Columbia				
	Fortune Island, Bahamas <sup>1</sup>	55 (1)	57 $\pm$ 13 (2)	0.96	1.03 $\pm$ 0.06
	Florida, St. John, British Honduras, Bahamas, Puerto Rico <sup>2</sup>	78 $\pm$ 3 (4)	76 $\pm$ 7 (10)	1.06	
<b>Pomacanthidae</b>					
<i>Molacanthus tricolor</i>	Salt River Canyon	152 $\pm$ 32 (2)	111 $\pm$ 10 (4)	1.37	
	St. Lucia, St. Vincent, Bahamas, Cuba, Bermuda <sup>1</sup>	156 $\pm$ 32 (3)	104 $\pm$ 21 (10)	1.50	1.44 $\pm$ 0.07
	Florida, St. John	135 $\pm$ 23 (10)	82 $\pm$ 27 (13)	1.44	

### 3. Agonistic Behavior

Three times unpaired males attempted to court a paired female and were chased away by the paired male. Some attacks were preceded by the paired male returning the parallel display. A more common agonistic encounter occurred between two pairs during the spawning period on five occasions. As a pair moved about their home range prior to spawning they encountered conspecific pairs, presumably near range boundaries. Since females usually lead the pair, they were the first to encounter the second pair. Fin-erect lateral displays were exchanged before members of the pair attempted to chase away the interloper(s). It appeared that, generally, the pair with the largest individuals prevailed during such encounters.

### 4. Courtship and Mating

Reproductive behavior of *C. capistratus* was studied at Salt River Canyon at depths between 15 and 20 m, and at the Channel patch reefs in 10 m of water (Fig. 1). Spawning behavior of 9 *C. capistratus* pairs was recorded during the dusk crepuscular period of 6 of 20 evenings (Fig. 2). No spawning of any chaetodontid or pomacanthid fishes was observed at any time but near sunset during our observations at all times of day and night. 7 spawns of *C. capistratus* were within four days before full moon, and two were within 9 days before full moon. Courtship behavior occurred without spawning on five occasions during other phases of the moon. On nights when spawning

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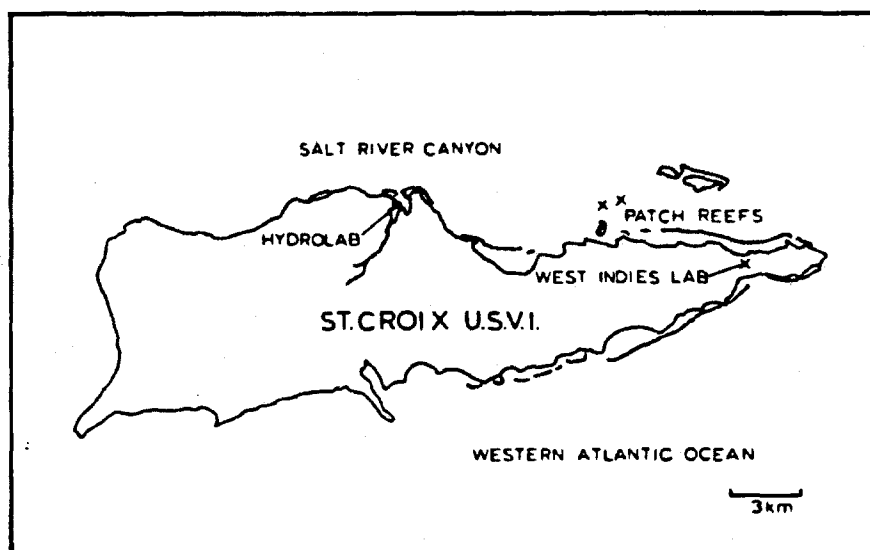


Fig. 2: Spawning observations of butterfly and angelfishes at St. Croix. Timing relative to sunset (solid line) and lunar phase. Spawning by all species ( $N = 19$ , 3 species) before sunset  $3 \pm 8$  min ( $\bar{X} \pm SD$ )

occurred, foraging rate decreased about 45 min prior to sunset when males began swimming closely behind their females. Periodically, the pair swam up from the bottom and presented a coordination display, orienting parallel to one another while erecting all fins as if to increase apparent size.

All observations of spawning were within the pairs' home range above a tall, conspicuous reef feature, such as the gorgonid *Pseudoplexaura*, or the coral *Acropora cervicornis*. Close circling, or carouselling (REESE 1975) began as soon as the female swam above the spawning structure. The male nudged the female's anal/abdominal region with his snout which led to almost instantaneous positioning of her above him. The female's head was pointed upward at about a  $20^\circ$  angle and sometimes she listed to the side. Males remained below and/or to the side of the female and both fish quivered as gametes were released. Depending upon the observer's orientation to light, milt could sometimes be seen as a small white cloud. Pairs spawned only once per evening. Immediately after spawning, the pair darted back down to the reef substratum. Combined duration of courtship and spawning was 2–6 min. Both sexes varied the intensity of their coloration while courting and mating. On three occasions, changes into nocturnal coloration occurred within 10 min after sunset. This coloration included a blanching of the eye mask, a white ring around the eye, and a dark dorso-ventral band about 1.5 cm wide just behind the pectoral fins.

Although *C. capistratus* is usually seen in pairs (Table 2) we observed pairs break up and reform with other individuals one evening when there was no spawning. At the full moon on 1 March 1980, two observers devoted the



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entire observation period to following two particular pairs and recording all reproductive behavior. Neither observer was able to stay with both pair members since they split up and reformed several times. Pairs began courtship with the coordination display but no carouselling or spawning occurred. Solitary individuals would display to a paired female and several times the female left her mate and joined the interloper. In other instances, the intruder was chased away.

#### B. *Chaetodon aculeatus*

##### 1. General Ecology

*Chaetodon (Prognathodes) aculeatus* is a predator of polychaetes, especially serpulid worms, crustaceans, and fish eggs for which it forages on the undersurfaces of corals, on sponges, and from algal turf (BIRKELAND and NEUDECKER 1981). *C. aculeatus* forages solitarily (Table 2) during the day in a specific home range and remains inactive there at night. The mean abundance of *C. aculeatus* for counts taken in 1978 was  $1.2 \pm 0.8$  individuals per 200 m<sup>2</sup>, which accounted for  $23 \pm 14\%$  of chaetodontid and pomacanthid fishes.

##### 2. Size Dimorphism

Males of *C. aculeatus* tend to be 7% larger than females (Table 3). The greater dimorphism of *C. aculeatus* than *C. capistratus* may partly result from the weaker association of pair members. Males initiate courtship and larger size may be important for this function.

##### 3. Courtship and Mating

Spawning behavior of *Chaetodon aculeatus* was observed twice in Salt River Canyon and courtship without spawning was observed on three other occasions. Both spawning events climaxed within 15 min of sunset during a new moon period (Fig. 2). Spawning was observed on 13 and 15 February 1980, a period of new moon, and did not occur on 20–22 February, during the moon's first quarter, nor after the full moon on 3 March 1980. Thus, while we observed courtship by *C. aculeatus* on nights when *C. capistratus* spawned, the congeners apparently did not spawn at the same time.

Mates maintained adjacent home ranges and met at the same spawning site each evening before sunset. We judged the sexes of individuals by their reproductive role. The male swam into his mate's home range about 40 min before sunset. All spawning activity began and climaxed above a large black coral (*Antipathes*) colony which grew up and outward over a large buttress at 18 m on the eastern slope. Upon meeting each evening, the pair performed a coordination display. This was followed by parallel swimming for one to two minutes. This coordination display occurred on several nights without reproduction. One evening the pair sporadically fed upon the *Antipathes* colony while swimming around it. Whenever the pair became separated by more than two meters, they displayed when rejoined. On evenings when spawning occurred, the female was noticeably swollen with roe.

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The spawning behavior of *C. aculeatus* was very similar to that exhibited by *C. capistratus* except that it was more prolonged. Courtship lasted between 10 and 15 min and parallel swimming gradually escalated into carouselling, with the female in front and the male close behind. As with *C. capistratus* the male approached the female from below and nudged her abdomen with his snout and, while carouselling, the pair ascended less than a meter above the *Antipathes* colony. The female stopped in the water column and oriented her head upward at about a 20° angle. The male swam underneath her at a similar angle and both fish quivered for about one second while releasing eggs and sperm. The pair spawned only once an evening, separated soon after releasing gametes and returned to their respective home ranges for the night.

### *C. Holacanthus tricolor*

#### 1. General Ecology

*H. tricolor* was the most abundant pomacanthid in Salt River Canyon ( $1.2 \pm 0.8$  individuals/200 m<sup>2</sup>) and accounted for  $12 \pm 13\%$  of sampled fishes. Dispersed groups of individuals remained in specific territories for the duration of our observations. Groups observed at dusk consisted of one large individual and 3—4 smaller ones, but individuals foraged solitarily during the day (Table 1) primarily on sponges (RANDALL and HARTMAN 1968) in territories which were defended by the large male. During 5-min foraging observations (N=8), *H. tricolor* fed on sponges (e.g. *Callyspongia*, *Verongia* 76% of all bites) and in the algal turf (21% of bites). Stomach content analysis showed mean % of diet volumes as 98.25 % sponge and 1.75 % algae (N=6).

#### 2. Sexual Dimorphism

Males of *H. tricolor* averaged 44 % larger than females (Fig. 3, Table 3). Within any single harem the male was the largest individual. There were no males smaller than 93 mm and most were larger than 120 mm. A few females were larger than 120 mm (5 of 37) but the vast majority (32 of 37) were smaller than 100 mm.

#### 3. Courtship and Mating

Spawning of *H. tricolor* was observed four times at Salt River Canyon and four times at the patch reefs. All spawns occurred within 8 days before the full moon (Fig. 2). *H. tricolor* is polygynous, as are some Pacific pomacanthids (LOBEL 1978; MOYER and NAKAZANO 1978). Entire spawning sequences (dominant male and all females) were observed only twice. As a result our data tend to underestimate total spawns per evening per male. 6 spawns climaxed less than 16 min before sunset ( $X = 11 \pm 7$  min), and the remainder climaxed less than 7 min after sunset. Males of *H. tricolor* were significantly larger than females (Table 3) and during spawning one male was accompanied by 2—4 females which lived in his territory.

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Fig. 3: *Holacanthus tricolor* mating. The male is the larger fish on the bottom. The male nudges the female with his snout against her lower abdomen just before gametes are released

About 35 min prior to sunset the large male began to swim around his territory and display to females. The male approached females in an undulating manner by listing back and forth on his side and presenting lateral displays with erect fins. One male appeared to visit and display to all females in his territory while making his way to his spawning site. Often these sites were the largest colonies of the gorgonid *Pseudoplexaura* in the territory. The male then began to court a female with additional listing and lateral displays and by swimming in ascending circles above her. If the female did not ascend, the male returned to her and continued to display. Usually this courtship included false spawns, in which the female moved up over the tower but then darted back to the substratum when the male attempted to position himself beneath her. In these cases the male followed the female and continued his courting. Once above the structure, and ready to spawn, the female allowed the male below her and he nudged her in the anal/abdominal region with his mouth and forehead while pushing her upward until the pair was 0.5–1 m above the tower. While spawning, the female remained nearly perpendicular to the bottom, and the male stayed below her with his head upward at about a 50° angle (Fig. 3). Both fish quivered while releasing their gametes. Immediately after spawning the fish darted back to the bottom; sometimes the female chased the male. Females spawned only once but the male spawned with two or more females each evening.

From the harem mating we observed, their apparent sex ratios, and the consistent pattern of male-female size dimorphism, we infer that *Holacanthus tricolor* is a protogynous hermaphrodite.

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#### D. *Pomacanthus arcuatus* and *P. paru*

##### 1. Courtship

Our observations of *P. arcuatus* and *P. paru* in Salt River Canyon (Table 2) show that both species generally occur as pairs although more strongly for *P. paru*. The fewer number of *P. arcuatus* pairs is probably a reflection of the distance paired individuals maintain and the resolution of the transect counts ( $> 2$  m would be scored as solitary). However, our observations throughout the Caribbean indicate that adults of both species generally occur as pairs which appear closely matched in size.

On several occasions during dusk in Salt River Canyon, when chaetodontids and *Holacanthus tricolor* were spawning, courtship behavior of *Pomacanthus arcuatus* and *P. paru* was observed, although spawning was not. The same general pattern of courtship behavior was exhibited by both species.

Between 30 min before and 10 min after sunset, on several nights, pairs were observed as they swam back and forth along our 100 m transect at 30 m. Individuals of these pairs were nearly equal in size and remained close together as they swam parallel to each other. Several times one of the pair listed over to one side and swam nearly perpendicular to its mate, exposing its ventral surface. These courting passes took place about 5 m above the bottom, covered distances greater than 100 m, and were not oriented above any particular topographical feature. *Pomacanthus arcuatus* was recently observed spawning 30 min before sunset, five days before a full moon in Puerto Rico (PAT COLIN, pers. comm.). COLIN described a long, horizontal spawning rush with only slight upward orientation when gametes were released. Our observations of *P. paru* suggest that it also spawns in a similar manner at dusk.

#### Discussion

##### A. Abundance and Distribution of Fishes and Their Prey

Abundance of *C. capistratus* is positively correlated with relative coral cover (Table 1,  $r^2 = 0.95$ ,  $p \leq 0.05$ ) and that of *H. tricolor* is positively correlated with amount of sponge surface area ( $r^2 = 0.90$ ,  $p \leq 0.05$ ). Abundance of *C. aculeatus* is also probably related to prey availability but was not demonstrated by our analysis because their small, elusive prey were not adequately sampled (BIRKELAND and NEUDECKER 1981). However, it seems probable that more prey and shelter sites were available to *C. aculeatus* on the west wall as a result of its greater structural complexity, and significantly more fish of this species occurred there than on the east slope.

Throughout Salt River Canyon corals were much more abundant in colony number and surface area than sponges (Table 1). The most abundant coral, *Agaricia*, forms continuous tabular colonies, whereas some sponges occur as large, discrete colonies such as the tubular *Callyspongia* or the vaseform *Verongia*. *C. capistratus*, a corallivore, was the most abundant species of chaetodontid and pomacanthid fishes, and was much more abundant than the sponge feeder *H. tricolor* (Table 1). The relationships of abundance suggest that

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*H. tricolor* territories could vary in quality and should be larger than home ranges maintained by *C. capistratus*. As a result of relative scarcity of sponges and their somewhat discontinuous distribution, *H. tricolor* males could defend these limited food resources, facilitating polygyny by making it advantageous for females to share high quality territories (ORIAN 1969). Polygyny could also result if female recruits form groups because they choose males which exhibit certain morphological or behavioral traits (cf. BURLEY 1981).

#### B. Disclaimer

In the following discussions we consider the evolution of monogamy and polygyny in fishes which spawn planktonic eggs and exhibit no parental care. We feel that a different set of selective pressures are responsible for mating system evolution in fishes which are viviparous or lay benthic eggs. Patterns of parental care influence development of mating systems (PERRONE and ZARET 1979; WITTENBERGER and TILSON 1980) and we divorce our arguments from those. Some relevant comparisons can be made with acanthurids, labrids, and scarids.

#### C. Social Groups

We call *C. aculeatus* and *C. capistratus* home ranging species (REESE 1973, 1975) because we have not seen defense of their feeding areas during the day. Observations of *C. capistratus* attacked and chased by damselfishes were common, but the butterflyfish simply moved on. In fact, territorial behavior is atypical for chaetodontids since it has been reported in only 4 of 93 extant species. The territorial species *C. baronessa* and *C. trifascialis* (REESE 1973, 1975), *C. fascialis* (FRICKE 1966), and *C. larvatus* (ALLEN 1980: 193), defend small reef areas, often a single coral head (REESE 1975). We did observe some conspecific aggression during spawning and over resting sites (cf. EHRLICH et al. 1977). Pomacanthids are more typically aggressive and territorial (LOBEL 1978; MOYER and NAKAZANO 1978; ALLEN 1980: 246) than chaetodontids (REESE 1973, 1975).

Foraging patterns, prey distribution and abundance exert considerable influence on social behavior in these fishes. *C. capistratus* apparently forms long-term pairs as suggested by the fact that 75 % of all individuals observed were paired (Table 2). Pairs fed only within their respective home ranges, generally remained within 0.5 m of each other, but rarely fed upon the same coral simultaneously. Foraging in pairs has less effect on feeding efficiency when sessile organisms are browsed because escape from predators is more difficult. In contrast, 91 % of *C. aculeatus* foraged solitarily (Table 2). Increased efficiency from solitary hunting of cryptic, motile crustaceans and prey with effective predator avoidance mechanisms may outweigh benefits of permanent pairing.

#### D. Evolution of Chaetodontid Monogamy

Relative costs to pairs may be lower than those imposed on solitary individuals of (1) ever ready sexual access, (2) less exposure to predators or

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increased defense, and (3) maintenance of home range resources. Constant mate availability within a home range avoids increasing the risk of predation during mate location outside a known area and of home range usurpation while gone. Continual presence of a mate would be advantageous when conspecifics are scarce. In Puerto Rico groups of up to 20 *C. capistratus* have been seen at dusk courting but not spawning, perhaps suggesting that monogamy may be related to this species' abundance on a reef (PAT COLIN, pers. comm.).

Solitary females of the acanthurid *Acanthurus leucosternon* were not as territorial and had a lower reproductive fitness than paired females (ROBERTSON et al. 1979). *C. capistratus* pairs seldom actively defended their home ranges during the day but did appear to constantly range over their area, monitor borders, and display to conspecifics. REESE (1975) suggested that the low amount of agonistic behavior among chaetodontids results from fishes knowing each other as individuals in conjunction with advertisement displays, which allow them to maintain social relationships on the reef with only an occasional bout of reinforcing agonistic behavior.

Current sexual selection theory argues for mate desertion after spawning when parental care of progeny is absent (TRIVERS 1972). How then is long term monogamy explained for fishes who spawn planktonic eggs which receive no parental care? While it may appear that male chaetodontids would benefit by deserting females after spawning to seek additional matings, the temporal synchronization of spawning throughout local populations is a major constraint. In other words, mating is restricted to a narrow time window which begins to slam shut after sunset. Thus, to be successful, a male would be required to mate and desert a female, and then locate and mate another one. But since continuously paired species, such as *C. capistratus*, are distributed on what appear to be nonoverlapping, exclusive home ranges, the availability of unpaired females is low. If paired females were pursued they would have to be fought for, as evidenced by the chasing of interloping males by paired males.

#### E. Effects of Pomacanthid Polygyny

In nonmonogamous bird species, the amount of time and energy devoted to display and associated activities is much greater than that in monogamous species, and male displays are exaggerated in both and repertoire (SELANDER 1972). Males of polygynous bird species have a greater variety of vocal signals than do females (ORIAN and CHRISTMANN 1968), whereas in monogamous species each sex has the same number of signals (SELANDER 1972). Similarly, the monogamous chaetodontids exhibited less complex reproductive behavior than did the polygynous pomacanthid, *Holacanthus tricolor*.

In polygynous systems with separate sexes (gonochores), including virtually all vertebrates, males acquire harems or mates mainly by winning in male-male competition. In the polygynous, protogynous hermaphrodite, *H. tricolor*, harem males are winners of intrasexual competition, but this competition occurs between females vying to change sex and become male. Such competition may be manifested as a race to increase size, but still females succeed

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by exhibiting the aggressive behavior of males. Consequently, floater (unmated) males do not exist as such because the male sex only results from sex change of large, aggressive females. Therefore, a dominant male competes for reproduction with all potential males which remain females by social inhibition. There is strong pressure for harem females to increase in size and aggressiveness and thereby challenge males. This effect is partly evidenced by female hesitancy to spawn (*H. tricolor*) and by the daily agonistic encounters between dominant males and harem females exhibited by *Centropyge interruptus* (MOYER and NAKAZANO 1978). The important difference between typical polygynous mating systems of gonochores and these hermaphrodites is that floater males (those without territories) in the former realize practically zero reproductive fitness, whereas potential males in the latter are reproductively active females. Harem male is the most fit reproductive tactic, even though it is a costly one because of time and energetic costs of territory and female defense. Females can "hedge their bet" by assuring some reproductive fitness before gambling on the big payoff, sex change.

Other factors may allow females to change sex besides death of the dominant male. For *H. tricolor* all recruitment to harems is probably by juveniles, which are exclusively females. There is no evidence to suggest that adults migrate <sup>within</sup> or between reefs. A male can spawn with a limited set of females a night, which places an upper boundary on harem size. Recognition of the importance of adult female-to-male sex ratio and only female immigration have led SHAPIRO and LUBBOCK (1980) to construct a theoretical model which allows female sex change and formation of subgroups when immigration to a group pushes the adult sex ratio beyond a threshold number. Whereas models of sex change in sequential hermaphrodites have often been based on attaining a critical size or age (SMITH 1967; CHOAT 1969; FISHELSON 1975), and on the release of suppression (ROBERTSON 1972), the SHAPIRO and LUBBOCK (1980) model accounts for some sex change as the result of the proximate social factors within groups. Social control of sex change has been experimentally demonstrated for *Thalassoma duperrey* in Hawaii (ROSS 1981). Female sex change to male was stimulated by the presence of smaller conspecifics, but inhibited by the presence of larger females (ROSS 1981). In the absence of other female conspecifics, isolated *Thalassoma duperrey* females did not change sex regardless of their age or size. Therefore, attaining a certain age or size per se does not result in automatic sex change; what is important is an individual's relative size within a group. This explains why females larger than males were found in collections of individual *H. tricolor* from multiple harems (Table 3), and predicts that in separate harems large females live with larger males, and conversely, small males live with even smaller females.

Once polygyny evolved it is easy to comprehend how this mating system could perpetuate. Female recruits play an ascendancy game to become harem male that promotes female groups. Recruits should choose harem sizes which offer the best chance to become males. In environments saturated with fish and where resource patches vary greatly in quality, harems at threshold size should be preferred. In poorer quality environments that cannot support

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groups, pairs should be more common. LOBEL (1978) related sex ratios (pairs versus harems) of *Centropyge potteri* to habitat defensibility such that harems formed on discrete, defensible reef patches. Similarly, *Centropyge interruptus* forms harems in habitats with maximum shelter and unstable monogamous pairs in less structurally complex habitats (MOYER and NAKAZANO 1978). Although pairs may be preferred in unsaturated environments, the probability of a recruit encountering a solitary male is low because males only result from sex change which requires interaction with conspecifics.

#### F. Sequential Hermaphroditism and Polygyny as Barriers to Adult Transfers

Extending the logic of harem-sex ratio threshold (SHAPIRO and LUBBOCK 1980) and only recruitment of juvenile females, several interesting predictions can be made. A dominant male controlling a threshold size harem should attempt to exclude all immigrants. Females should assist all smaller recruits to expedite their own sex change. While many authors have evoked an increased risk of predation to explain the lack of adult transfer within or between reefs, we envision a social constraint. In polygynous hermaphrodites, large fish attempting to join groups should be repelled by group members. Therefore, group social pressure may also be an important constraint on adult transfers within or between reefs.

#### Summary

*Chaetodon aculeatus* foraged solitarily during the day for elusive prey and mated in pairs with nearby individuals at dusk. Pair formation occurred at the same site each evening, even without spawning. Considerable amounts of time were devoted to greeting and females returned displays initiated by males. Courtship lasted between 10 and 15 min and culminated with a close carrouselling ascent, anal nudging and one gamete release per evening.

*C. capistratus* formed permanent pairs which foraged together diurnally in home ranges, bred there at dusk, and remained inactive there at night. Courtship lasted only 2–6 min but included the same display repertoire exhibited by *C. aculeatus*. Females played active roles in courtship. Pairs began courting within 20 min of sunset and spawned once per evening.

These chaetodontids are site-attached reef fishes that maintain exclusive use of certain resources contained within permanent home ranges. These use patterns have probably allowed the evolution of monogamy because of lower costs of home range maintenance for pairs and easy sexual access. Pairs of the more monogamous species, *Chaetodon capistratus*, spawned once per evening, and courtship was uninvolved. *C. aculeatus*, which foraged solitarily during the day and joined a nearby mate at sunset, exhibited a relatively prolonged courtship, although the display repertoire was the same. In contrast, the polygynous species, *Holacanthus tricolor*, had an involved courtship consisting of a diverse repertoire. These differences were not limited to courtship complexity. Chaetodontid males and females presented and returned courtship



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displays, whereas *H. tricolor* females were hesitant and often did not spawn unless a male displayed repeatedly.

The monogamous species are not dimorphic in size and spend considerably less time and effort on courtship than does the polygynist. Since *C. capistratus* pairs are continuously together, courtship serves primarily to synchronize gamete release. The less closely associated pairs of *C. aculeatus* spend more time on greeting and pair formation before spawning. Female chaetodontids reciprocate the displays given by males. Males of *H. tricolor* are 44 % larger than females, exhibit more displays than chaetodontids, and present them more frequently to females. Females often require males to repeat their displays before spawning and seldom return displays. *H. tricolor* males must continuously reaffirm their dominance, especially to large females, because of their immediate challenge as potential males. Females play their sex role because it is a complementary reproductive tactic which guarantees some fitness at a relatively low cost compared to the high cost, albeit high payoff, male tactic. Because of the harem mating system of *Holacanthus tricolor*, the apparent excess of females, and the consistent pattern of male-female size dimorphism, we conclude that *H. tricolor* is a protogynous hermaphrodite.

Overall, spatial and temporal patterns of spawning behaviors of chaetodontid and pomacanthid fishes support zygote and adult antipredation hypotheses (JONES 1968; JOHANNES 1978; LOBEL 1978). Gametes are released above structures that place them above foraging diurnal planktivores and offer adults refuge from predators. Spawning culminates near sunset, a time when the primary zygote predators are becoming inactive and beginning an interlude of planktivore inactivity. Later, nocturnal planktivores begin to feed, but they take few of the then abundant zygotes (HOBSON and CHESSE 1978). For some species spawning intensity appears to peak during the week prior to the full moon, another correlate of zygote avoidance of predators, since tidal exchanges are maximum then.

#### Zusammenfassung

*Chaetodon aculeatus* schwimmt tagsüber solitär Nahrung suchend umher, gegen Abend schließen sich Paare zusammen, auch ohne abzulaichen. Paare zeigen langdauernde Begrüßungsrituale. Die Balz währt 10–15 min und endet mit einem Abulaichen je Abend.

*C. capistratus* bildet Dauerpaare, die tagsüber zusammen fressen, abends laichen und nachts am selben Ort inaktiv sind. Die Balz enthält dieselben Elemente wie bei der vorigen Art, dauert aber nur 2–6 min. Paare beginnen mit der Balz 20 min vor Sonnenuntergang und laichen nur einmal je Abend.

Beide Arten sind ortstreue Riffbewohner, die von ihrem Streifgebiet leben, das sich wohl von einem monogamen Paar leichter erhalten läßt. *C. capistratus* laicht mit wenig Balz, *C. aculeatus* nur nach langer Balz, an der das Weibchen stark beteiligt ist; das Männchen von *Holacanthus tricolor*, einer polygenen Art, muß seine Balz oft mehrfach wiederholen bevor das Weibchen einwilligt. Hier ist das Balz-Repertoire größer und braucht mehr Zeit als bei den monogamen Arten, die nicht sexual-dimorph sind. *H. tricolor*-Männchen

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sind 44 % größer als Weibchen. Je ähnlicher die Paar-Partner sind und je länger sie sowie beieinander sind, desto kürzer fällt die Balz aus, die wohl vornehmlich der Synchronisation dient. *H. tricolor* ist wahrscheinlich ein protogynher Hermaphrodit, bei dem das Männchen-Individuum sich mit viel Aufwand die Dominanz sichern muß, um hohen Fortpflanzungserfolg zu haben.

Abgelaicht wird generell an Orten und zu Zeiten, die geringe Gametenverluste versprechen: Über den Strukturen, die tagaktive Planktonfresser tragen, und in der Abenddämmerung, wenn Planktonfresser inaktiver werden. Nächtliche Planktonfresser werden erst später aktiv. Einige Arten scheinen bevorzugt in der Woche vor Vollmond zu laichen, wenn die Gezeitenbewegungen besonders stark sind und die Zygoten verteilen.

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